Assessing the effects of architectural variations on light partitioning within virtual wheat – pea mixtures

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ABSTRACT

Background and Aims Predicting light partitioning in crop mixtures is critical to improving the productivity of such complex systems. Furthermore, light interception has been shown to be closely linked to plant architecture.The aim of the present work was therefore to analyse the relationships between plant architecture and light partitioning within wheat-pea mixtures. To address this issue, we used an existing model for wheat (Fournier *et al.*, 2003) and developed a new model for pea morphogenesis. Both models were then used to assess the effects of architectural variations in light partitioning.

MethodsFirst, a deterministic model (L-Pea) was developed in order to obtain dynamic reconstructions of pea architecture. L-Pea model is based on the L-systems formalism and consists of modules for ‘vegetative development’ and ‘organ extension’. A tripartite simulator was then built up from pea and wheat models interfaced with a radiative transfer model. Architectural parameters from both plant models, selected on the basis of their contribution to Leaf Area Index (LAI), height and leaf geometry, were then modified in order to generate contrasting architectures of wheat and pea.

Key results By scaling-down our analysis to the organ scale, we showed that the number of branches/tillers and length of internodes markedly determined the partitioning of light within mixtures. Temporal relationships between light partitioning and the LAI and height of different species showed that light capture is mainly related to the architectural traits involved in (i) plant LAI during the early stages of development, and (ii) plant height during the onset of inter-specific competition.

Conclusions*In silico* experiments enabled to study of the intrinsic effects of architectural parameters on the partitioning of light in mixtures. Our findings showed that plant

architecture is an important criterion for the identification/breeding of plant ideotypes, particular with respect to light partitioning.

Key words:architectural parameters, Functional Structural Plant Model, intercropping, LAI, light interception, L-Systems, *Pisum sativum* (pea), plant architecture, plant height, *Triticum aestivum* (wheat)

INTRODUCTION

In the current context of improving the sustainability of agriculture, there is renewed interest in the growing of crop mixtures, referred to as intercropping (Willey, 1979, Anil *et al.*, 1998). Crop mixtures can indeed produce high and stabilized yields; they can also enable a reduction in the use of fertilizers and pesticides and enhance biodiversity conservation (Ofori and Stern, 1987, Jensen, 1996, Corre-Hellou *et al.*, 2006, Malézieux *et al.*, 2009). These benefits result from the trade-off between the complementarity and competition between mixed species with respect to resource capture and use. In particular, the ability of component species in the canopy to capture light strongly determines both their potential productivity and their proportion in the mixture at harvest. Understanding the modalities of light partitioning is therefore a crucial area of study.

The partitioning of light among mixed species is closely linked to their temporal and spatial development. On the one hand, the period of time where one of the crops has not yet developed has important effects on the partitioning of light and hence on growth of the mixture. These situations are notably encountered in relay cropping(Malézieux et al., 2009)wheremixed crops do not grow simultaneously but tend to exhibit a partial overlap (*e.g.* maize-beans, groundnut-cotton). On the other hand, the interception of light by plant stands is also closely related to the physical structure of the canopy (Ross, 1981a, Sinoquet and Caldwell, 1995) which itself is determined by the architecture (Godin, 2000) of the individuals growing within the stand (Moulia *et al.*, 1998). Such a multi-scale description of canopy structure highlights the fact that architectural parameters defined at the organ scale can significantly affect light partitioning. Unlike homogeneous monospecific stands, where plants have roughly the same architecture, intercropping systems involve at least two species which may display differing architectural patterns (*e.g.* agroforestry systems, cereal–legume mixtures). Characterising the architecture of intercropped plants, and its variability (genotypic

and environmental) is therefore a critical issue that could guide the choice of the species/cultivars to be mixed in intercropping systems and hence their degree of complementarity (Sinoquet and Caldwell, 1995, Sonohat *et al.*, 2002).

Exploiting the variability of plant architecture is of great interest in the context of intercropping systems; however, few methods are available to assess and quantify the impact of different architectural patterns on the partitioning of light between mixed species. To the best of our knowledge, and because of experimental and cost constraints, light partitioning within interspecific mixtures cannot be assessed directly by radiation sensors (Sonohat *et al.*, 2002). The only feasible alternative at present is a modelling approach that involves various concepts and formalisms for (i) representation of the canopy and (ii) the calculation of light interception. Most studies are based on the turbid medium approach where the canopy is represented using a statistical model and light interception is given by Beer-Lambert's law (Sinoquet *et al.*, 1990, Monsi and Saeki, 2005). The turbid medium paradigm has thus been applied to several intercropping systems such as pea–barley (Corre-Hellou *et al.*, 2009), maize-bean (Tsubo and Walker, 2002, Tsubo *et al.*, 2005), perennial mixtures (Faurie *et al.*, 1996, Lantinga *et al.*, 1999) or agroforestry systems (Noordwijk and Lusiana, 1999). These approaches were based on a simplified description of the canopy given by integrative parameters such as Leaf Area Index (LAI), plant height and mean leaf inclination. However, due to their underlying hypotheses, crop models coupled to the turbid medium approach cannot explicitly account for plant architecture *sensustricto*. Therefore, such models are not suitable to assess the relationships between light partitioning and architectural parameters (organ scale) of the component species. Moreover, the turbid medium analogy applied to intercropping systems has also been shown to produce inaccurate estimations of light partitioning in some complex canopy structures (Sonohat *et al.*, 2002, Combes *et al.*, 2008, Barillot *et al.*, 2011). Furthermore, alternative modelling concepts such as functional–

structural plant models (FSPM), are able to take account of interactions between plant architecture, their physiological functioning and environmental conditions (for a review see: Fourcaud *et al.*, 2008, Vos *et al.*, 2010, DeJong *et al.*, 2011). FSPMs therefore represent a suitable framework to understand the modalities of light partitioning within intercropping systems. Such approaches have been used to quantify light partitioning within contrasting canopies: agroforestry (Lamanda *et al.*, 2008), a legume-weed system (Cici *et al.*, 2008) and grass-legume mixtures involving perennial and annual species (Sonohat *et al.*, 2002, Barillot *et al.*, 2011).

The aim of the present study was therefore to investigate the influence of architectural variations on the partitioning of light among mixed species using a FSPM approach. To achieve this, we decided to use grass-legume mixtures, a commonly used intercropping system in temperate regions (*e.g.* wheat-pea, triticale-broad bean, tall fescue-alfalfa) and tropical zones (*e.g.* maize-bean). Our approach consisted in using a wholly *in silico* framework based on dynamic architectural models of both the species in a grass-legume mixture. For the grass species, we used an existing wheat model (ADEL-Wheat, Fournier *et al.*, 2003), while for the legume species, we chose pea for which we developed a new model. Both models were combined to analyse the effects of architectural changes on the level of light partitioning in virtual wheat-pea mixtures. These architectural models do *not* account for any plastic responses of plants to their environment. This approach thus enabled us to assess the intrinsic effect of specific architectural traits on the partitioning of light.

MATERIALS AND METHODS

Description and parameterization of the L-Pea model

The virtual plant model for pea (L-Pea) was developed using the L-Py platform (Boudon *et al.*, 2012) which combines the formalism of L-systems (Lindenmayer, 1968,

Prusinkiewicz and Lindenmayer, 1990) with Python, an open source and dynamic programming language. The structural organisation of stems was described as a modular system (Godin *et al.*, 1999) *i.e.* as a collection of repeated basic units called *phytomers* (Gray, 1849, White, 1979). Using this formalism, the main vegetative organs of pea were represented by a bracketed string made up of the following modules: apex (apical meristem), A; internodes, *I*; stipules, *S*; and axillary buds *B*. Thus, the apex production rule used in the L-Pea model is:

$$A \rightarrow I\ [S]\ [S][B]_n\ A,$$

meaning that the initiation of a phytomer by the apex (*A*) is associated with the production ($\rightarrow$) of an internode (*I*), two stipules (*S*), *n* axillary buds (B) and an ongoing apex. Square brackets are topological rules that indicate branches. Each module (virtual organ) bears its own state *i.e.* identification (cultivar, plant, stem and phytomer to which they belong), age, length and amount of intercepted light.

In the model proposed here, the morphogenesis of pea is dependent on the growing degree day (GDD) cumulated since sowing (base temperature = 0°C). Thermal time drives the two main modules represented in the L-Pea model: (i) vegetative development and (ii) the extension of vegetative organs. Parameterization of the *vegetative development* module (Table 1) was derived from an experiment conducted under field conditions on pea (*cv* Lucy) intercropped with wheat. Details on growing conditions and measurements can be found in the article Barillot *et al*. (2014). Moreover, these data were completed by a supplementary experiment designed to characterise the extension kinetics of stipules and internodes. Measurements were performed on isolated pea plants grown in growth cabinets (see details in [**Supplementary Information**]).

Vegetative development module

Rate of phytomer appearance

The L-Pea model does not account *sensusstricto* for the initiation of vegetative primordia by the apical meristem (plastochron). In fact, the leaf appearance rate (R_L) as measured by Barillot *et al.* (2014) was used directly in the model to initiate the production of a new phytomer which immediately starts its visible growth *i.e.* no hidden growth period was considered. Therefore, the production and appearance of phytomers (concomitant events in the model) were implemented as a linear function of the leaf appearance rate:

$$Nphyto_{(p,s)}(t) = \min(R_{L\,(p,s)} * t,\ phyto\_final_{(p,s)}) \qquad \text{Equation 1}$$

where $N_{phyto(p,s)}(t)$ is the number of visible phytomers at a given thermal time t (*GDD*,Growing Degree Day from emergence) for plant p and stem s; parameter $R_{L(p,s)}$is the rate of leaf appearance used as the rate of phytomer appearance (phytomer C° day^{-1}); and $phyto\_final_{(p,s)}$ is the final number of phytomers. Parameters $R_{L(p,s)}$ and $phyto\_final_{(p,s)}$ are input parameters of the model which can be specified for each plant (p) and stem (s) *i.e.* main stems and each lateral branch. Note that the $phyto\_final_{(p,s)}$ of main stems measured in Barillot *et al.* (2014) was low so that the model could account for death of the apical meristem of main stems, which frequently occurs in winter pea cultivars that experience cold temperatures (Jeudy and Munier-Jolain, 2005, Barillot *et al.*, 2014).

Branching

Based on our previous experiment on intercropped pea (Barillot *et al.*, 2014), we only considered first-order branches. Branching is therefore handled by the model through two main input parameters (Table 1) which are: (i) the number of axillary buds (nb_branch_n) located at each node (n) of the main stem, and (ii) the time of bud break (bud_break_{rk}). Branches were denoted according to their topological position, *i.e.* main stems were denoted

as Axis-0, and then branches emerging from node *n*of the main stem were referenced as *Axis-n*. Properly speaking, the axillary buds should rather be called "active buds" as they represent those which actually lead to development of a branch and not the total number of buds. Based on the measurements made by Barillot *et al.* (2014), the L-Pea model was set with,

$$nb\_branch_n = \begin{cases} 2, & for\ 1 \le n \le 2 \\ 0, & for\ n > 2 \end{cases}$$

Organ extension module

Organ growth kinetics

The extension of internodes and stipules is assumed to follow a β function (Yin *et al.*, 2003):

$$L_{t,org} = \begin{cases} L_{final\ org}\left(1 + \frac{t_{end\ org} - t}{t_{end\ org} - t_{max\ org}}\right)\left(\frac{t - t_{base\ org}}{t_{end\ org} - t_{base\ org}}\right)^{\frac{t_{end\ org} - t_{base\ org}}{t_{end\ org} - t_{max\ org}}}, & \text{for } t < t_{end\ org} \\ L_{final\ org}, & \text{for } t \ge t_{end\ org} \end{cases} \quad \text{Equation 2}$$

whereL_{final} (mm) is the final organ length, t (°C day) the current age of the organ, t_{base} the beginning of organ extension (°C day), t_{max} (°C day) the time point at which the maximum rate of organ extension is reached, and t_{end} (°C day) is the duration of organ extension. The values for the parameters t_{base},$t_{max}$and t_{end} shown in Table 1 were normalized by the time of the first organ starting its extension in a phytomer. Our results showed that the development of phytomers was initiated by the emergence of stipules (t_{base} = 0°C day) which started to grow slightly earlier than internodes [**Supplementary Information**]. The final length reached by organs (L_{final}) is defined as a function of the normalised phytomer rank ([**Supplementary Information**]).

The width of stipules ($W_{stipule}$) at time *t*was derived from an allometric rule:

$$W_{t,stipule} = k * L_{t,stipule} \quad (R^2 = 0.95) \qquad \text{Equation 3}$$

where*k* is the allometric coefficient and $L_{t,stipule}$ is stipule length.

Senescence

In the L-pea model, shoot senescence only concerns stipules that are removed once their lifetime has elapsed (Table 1). The values for leaf lifespan were derived from Lecoeur (2005).

Geometric interpretation of the model

Internodes were associated to generalised cylinders. Stipules were reconstructed from a library of about 200 geometric objects obtained from the photographs used to extract stipule shape.

ADEL-Wheat model

Virtual wheat plants were obtained from a dynamic and 3D architectural model of wheat development (Fournier et al., 2003). This model is available on the Openalea platform (Pradal et al., 2008). The dataset was derived from an experiment carried out by Bertheloot et al. (2009) where wheat (cultivar Caphorn) was grown under field conditions with low nitrogen fertilization at a density of 250 plants m^{-2}. The model simulates the elongation kinetics of individual organs, and their geometric shape. The development and death of tillers was also accounted for in the model and was kept constant in our simulations.

The input parameters of both the ADEL-Wheat and L-Pea models used to build up the virtual mixtures were thus based on experiments with low nitrogen levels similar to those applied by farmers in Western Europe.

Virtual wheat–pea mixtures: interfacing the L-Pea and ADEL-Wheat models

The L-pea model was implemented on the Openalea platform so that it could be interfaced with ADEL-Wheat. Wheat and pea mock-ups were merged in scene graphs using the PlantGL graphic library (Pradal et al., 2009). Simulations were processed from 0 to 2000 GDD with a time step of 50 GDD (Table 2). The inter-row spacing of mixtures was 0.17 m, with a final density of 125 plants m-2 for wheat and 45 plants m-2 for pea *i.e.* 50% of the optimum density of each crop as generally encountered in Western European farming practices (Corre-Hellou et al., 2006). The component species were mixed within each row in virtual mixtures of 0.5x0.5 m (two rows including 18 wheat plants and 6 pea plants).

Light partitioning within virtual wheat–pea mixtures

The virtual wheat–pea mixtures were coupled with a radiative transfer model that estimates the dynamics of PAR partitioning at each step of the growing cycle. Calculations of light interception were provided by the nested radiosity model,Caribu, developed by Chelle and Andrieu (1998). The computations only considered diffuse radiations according to the Uniform OverCast (UOC) sky radiation distribution (Moon and Spencer, 1942). Diffuse radiations were approximated using a set of 20 light sources. Light interception by each organ was computed for each direction and then integrated over the sky vault by summing up the weighted values obtained from all 20 directions. In order to prevent any border effects, the basic mixture plot of 0.25 m^{-2} was duplicated using an option of the Caribu model.

Building contrasting wheat and pea architectures

The architectural parameters of both models were set initially to ensure the smallest possible difference of LAI and height dynamics between wheat and pea. This first simulation is hereinafter called the *reference simulation* (see detailed architecture in Table 3and Figure 1).

Architectural alterations were then applied to both plant models in order to quantify their impact on light partitioning throughout the growing cycle of the mixture. These architectural parameters were selected as a function of their contribution to the Leaf Area Index (LAI), plant height and leaf geometry. (i) Variations in LAI were obtained by increasing or decreasing the number of tillers and branches produced by wheat and pea, respectively. (ii) Variations in plant height were obtained by altering the final length of internodes. (iii) During previous studies (Barillot *et al.*, 2011, Barillot *et al.*, 2012), it was found that leaf inclination had minor effects on light partitioning within virtual wheat–pea mixtures when compared to the LAI and height of the species. In order to validate this assumption, light partitioning was also estimated within mixtures where the leaf inclination of pea was altered. Based on the initial values set for the reference simulation, 25% and 50% variations in both directions were applied to each architectural parameter.

All simulations were performed by modifying one parameter at a time, which thus represented a total of 21 simulations. The effects of each architectural parameter (*simul*) on plant LAI and height and on light partitioning were compared to the reference simulation (*Ref*) by calculating the relative variations:

$$Relative\ variation = (Ref - Simul)/Ref \quad \text{Equation 4}$$

Based on these simulations, we were able to analyse the relationships between light partitioning and variations in the species ratios of LAI and height. To this end, five particular stages during development were selected (see Table 2). The first dates represented the vegetative stages of the two species and onset of their lateral development (branching and tillering). Vertical elongation phases were then selected, as well as the flowering periods of wheat and pea. The relationships between light partitioning and species LAI and height were

finally studied during the last stages of development nearing physiological maturity (2000 GDD).

RESULTS

Reference simulation

The dynamics of LAI, height and light interception efficiency (LIE: the fraction of incident light intercepted by a species or the whole mixture) for the reference simulation are shown in Figure 2. Between 200 and 2000 GDD after sowing (Figure 2A), the LAI kinetics of the whole mixture and of each component species followed typical kinetics as of those observed in pea–barley mixtures (*e.g.*Corre-Hellou *et al.*, 2009). The mixture reached a maximum LAI of 6.30 at the time of wheat and pea flowering (1400 GDD). After 1700 GDD, the senescence of wheat and pea leaves gave rise to a fall in the mixture LAI to 4.45. Differences between the LAI of wheat and pea did not exceed 0.66.

Pea was taller than wheat from the early stages of development to 1000 GDD, a period which corresponds to the elongation of wheat internodes (Figure 2B). The stable height of pea observed between 800 and 1000 GDD could be explained by: (i) the death of the main stem, causing a cessation of vertical growth, and (ii) the delayed growth of branches that overtopped the main stems as from 1100 GDD and led to a final height of 0.70 m. The height of wheat also remained at 0.11 m between 400 and 700 GDD *i.e.* before internode elongation which resulted in a maximum height of 0.70 m.

The LIE of the mixture increased rapidly until the final height of species had nearly been reached (1500 GDD) and then stabilized at 0.9, meaning that 90% of incident light was intercepted by the canopy (Figure 2C). As a consequence of these greater LAI and height values, pea captured on average 62% of the light intercepted by the overall mixture up to

1100 GDD. The contribution of wheat to light interception by the mixture subsequently averaged 57% until 1700 GDD.

Variations in species LAI and height in response to architectural alterations

LAI variations

Alterations in the number of branches produced by pea dramatically affected its LAI from the early stages of development (400-500 GDD, Figure 3). Based on the reference simulation, similar *absolute* variations in LAI were observed after an equivalent increase or decrease in the number of branches, thus defining symmetric variations. As expected, the greatest differences in LAI were observed when the number of branches increased or decreased by 50% (+0.50 and -0.52, respectively).

Alterations in the number of tillers produced by wheat also led to strong relative variations in LAI, although the amplitude was less marked than in pea (Figure 3). These effects were observable from 600-650 GDD *i.e.* during tiller production. Maximum relative variations of +0.30 and -0.37 in wheat LAI were observed at the end of tillering (850 GDD) and resulted from a 50% increase or decrease in the number of tillers, respectively. Relative variations in LAI then rapidly diminished as from 900 GDD under each scenario. After flowering (around 1500 GDD), these plants even reached the same LAI values as those of the reference simulation. This was due to a parameter relative to tiller death which led to the same final number of tillers as the reference simulation because: (i) the tillers removed under the -25 and -50% scenarios were also intended to regress in the reference simulation, and (ii) the tillers added (+25 and +50% scenarios) were set to regress at the same time as those in the reference simulation.

Height variations

Symmetrical absolute variations in the height of pea and wheat were observed after an equivalent increase or decrease in internode length (Figure 4). Relative variations in pea height were constant from 800 GDD to the end of the growing cycle (maximum variations of 0.47 and -0.47 under the +50% and -50% scenarios, respectively).

The effect of internode length on plant height was observed later in wheat than in pea, as the elongation of wheat internodes started from 1000 GDD. Maximum relative variations were observed at 1400 GDD (0.33) and 1500 GDD (-0.31) consecutive to a 50% increase or decrease in internode length, respectively.

Effects of architectural modifications on light partitioning

Figure 5 shows (i) the effects of branching/tillering, internode length and leaf inclination (pea) on the fraction of light (%PAR) intercepted by a particular species over the interception of the whole mixture (values are thus complementary between pea and wheat), and (ii) variations in %PAR expressed as a function of the reference simulation. Interestingly, the modifications made to architectural parameters led to asymmetric responses of light partitioning even though they symmetrically affected LAI and plant height (same absolute variations observed after an increase or decrease in a given parameter). Indeed, increasing or reducing the value of an architectural parameter (branching, height, or leaf inclination) did not result in similar absolute variations in light partitioning but rather defined asymmetric responses.

Branching

Alterations to the number of branches/tillers led to greater variations in light partitioning in pea than in wheat. This was particularly the case when the number of branches was reduced as this dramatically decreased the proportion of light intercepted by pea from the

early stages of development (500 GDD). Reducing the number of pea branches by 25% or 50% caused maximum losses of light interception of 17% and 53%, respectively, just before the flowering stages (1250 GDD, Figure 5B). By contrast, increasing the number of branches resulted in smaller variations in light partitioning than those caused by their reduction (a 20% maximum gain of light capture under both the +25% and +50% scenarios). Compared to the branch modifications applied to pea, the number of wheat tillers led to slight relative variations in light partitioning (15% at most). The variations in wheat LAI which can be seen in Figure 3 (30-35 %) therefore had little effect on light.

Internode length

Modifications to internode length (Figure 5C and D) appeared to have the most dramatic effects on light partitioning when compared to branching (at most an 81% gain and a 65% loss in light capture). In both pea and wheat, longer internodes resulted in a marked increase in light interception when compared to the reference simulation. For both species, strong asymmetry was found regarding variations in light partitioning between plants subjected to an increase in their internode length and in those whose internodes were reduced, especially from 1500 GDD. From this stage of development, the effects of internode length which had caused a gain in light interception by pea (*i.e.* longer internodes for pea and shorter for wheat) started to decline until maturity. By contrast, alterations which increased wheat height (*i.e.* shorter internodes for pea and longer for wheat) maintained wheat dominance in terms of light interception until maturity. Figure 5D also shows that similar variations in light partitioning could result from an increase in the internode length of pea, or an equivalent reduction in wheat internodes. By contrast, increasing the internode length of wheat did not cause a similar gain in light interception as an equivalent reduction of pea internodes. Indeed, wheat was the most dominant species in terms of light capture when the internodes of pea were shortened by 25% or 50% (respectively up to 76% and 85% of light captured by wheat).

Increasing the internode length of wheat by 50% resulted in a similar gain in light interception than when the internode length of pea was reduced by 25%.

Leaf inclination of pea

Alterations to the inclination of pea leaves clearly had minor effects on light partitioning when compared to the changes applied to branching and internode length. Nevertheless, increasing leaf inclination by 50% (*i.e.* the leaves became more erect) reduced light capture of pea by 18% at most.

Light partitioning as a function of the ratios of species LAI and height

The results described above evidenced the dynamics of light partitioning in response to contrasting plant architectures. As illustrated in Figure 3 and Figure 4, such architectural alterations induced a broad range of variations in the LAI and height of the component species. The next step was therefore to analyse the relationships between light partitioning and variations affecting both ratios of species LAI and height (Figure 6). This analysis was performed at five particular stages of development (Table 2).

During the early stages of development (500 GDD), the architectural modifications made mainly affected the height of pea plants (Figure 3 and Figure 4). Therefore, the ratio of the species LAI (Figure 6) did not display any marked variations (except when the number of pea branches was reduced by 50%). By contrast, changes to the internode length of pea led to different height ratios, ranging from 1 to 1.92. Despite the reduction in its internode length, pea remained the dominant species in terms of light capture, mainly due to its higher LAI compared to wheat. At the end of the branching and tillering stages (850 GDD), wheat and pea developed contrasting levels of LAI in response to architectural variations (the LAI ratio ranged from 0.7 to 1.9). This resulted in marked variations in light partitioning as pea intercepted between 51% and 71% of the light captured by the whole mixture. Whether the

architectural variations were applied to pea or wheat, the LAI ratios were similar, although they are obviously affected in contrasting ways. Like the results observed at 500 GDD, light partitioning was also linked to the height ratio, which was modified by alterations made to pea internodes (wheat internodes had not started their elongation). The relationship between light partitioning and the LAI ratio no longer appeared to be linear at 1000 GDD. Indeed, increasing the number of branches/tillers still modified the LAI ratio but this only resulted in slight variations of light partitioning. However, the sharing of light among the component species was linearly related to the variations in height ratio which originated from modifications to the internode length of pea. Under these scenarios, light intercepted by pea ranged from 28% to 69% of the total light interception. At flowering (1500 GDD), the onset of internode elongation in wheat generated contrasting vertical dominance (the height ratio ranged from 0.63 to 1.20) which markedly affected light partitioning (between 15% and 70% of light captured by pea). Figure 6 also shows that alterations to internode length at 1500 and 2000 GDD led to similar absolute variations in height ratio and light partitioning, whether they were made to pea or wheat. The effect of the LAI ratio on light partitioning continued to decline at maturity (2000 GDD). The LAI ratio ranged from 0.48 to 1.45 but only increased the light interception of pea by 10%. Variations in the height ratio at this stage of development were similar to those observed at 1500 GDD. However, the link with light partitioning appeared to become non-linear, particular with the most marked alterations to internode length (±50%).

DISCUSSION

The L-Pea model: a deterministic approach to modelling the aerial morphogenesis of pea

For the purposes of our study, we developed a deterministic model that generate a simplified and dynamic representation of pea architecture. Pea morphogenesis was modelled

as a function of thermal time, in line with the work by Turc and Lecoeur (1997) who found stable linear relationships between thermal time and the number of expanded leaves in pea whatever the plant growth rate, cultivar and period of the cycle. As mentioned by Prusinkiewicz (1998), the design of developmental models necessitates the definition of rules to describe the emergence of new modules during development as well as the growth kinetics of modules produced previously. During the present study, these rules were considered in light of the results of two separate experiments, one conducted under field conditions (Barillot *et al.*, 2014) and the other in a growth cabinet. The latter measurements, dedicated to characterising stipules and internode elongation, were obtained on pea plants which had not been grown in a mixture with wheat. These kinetics were not therefore intended to accurately quantify the extension of pea internodes and stipules in an intercropping system, but rather to capture the main characteristics of their extension and coordination. Furthermore, the kinetics of organ extension were likely to have a limited influence on our results as we performed an analysis of the sensitivity of light partitioning to alterations in the number of branches/tillers and internode length.

Moreover, the L-Pea model was used to represent realistic/measured architectures of pea plants (resulting from the integration of environmental effects) but was not designed to reproduce the responses of plants to the environment. Indeed, the current version of the L-Pea model does not account for environmental influences on pea morphogenesis (*e.g.* intra/inter-specific competition, abiotic or biotic factors). Although this goes beyond the scope of this paper, future studies on the L-Pea model could be performed in order to develop a more mechanistic approach to pea development that might include feedback between the resource status of plants and their morphogenesis.

An *in silico* experiment to assess the effects of contrasting architectures on light partitioning within mixtures

An ability to manipulate light partitioning in multi-specific stands is crucial to managing the balance between component species and also determining the final yield of the mixture (Ofori and Stern, 1987, Keating and Carberry, 1993, Sinoquet and Caldwell, 1995, Malézieux *et al.*, 2009, Louarn *et al.*, 2010). The present work therefore focused on the architectural determinants (*i.e.* physical modalities) of light partitioning in intercropping systems, but did not aim to study competition for this resource. As a first step towards understanding competition for light within intercropping systems, *in silico* experiments were performed using two deterministic FSPMs of wheat and pea morphogenesis, without taking any account of the plastic responses of plants to their environment. The tripartite simulator (wheat-pea-light) built up for this study therefore represented a heuristic tool to assess the intrinsic effects of individual architectural parameters. More generally, this simulator could be used to test hypotheses that are inaccessible to "conventional" experiments because of technical or time constraints. Although the environmental responses of plants were not taken into account, the contrasting architectures of plants that were generated during this work could mimic the situations encountered in different intercropping systems subject to particular environmental conditions (*e.g.* agroforestry systems where one species largely overtops another).

By scaling-down our analysis to the organ scale, this study provided novel information on the temporal sensitivity of light partitioning to the architecture of component species. Some previous works had also aimed to analyse the relationships between light partitioning and the simplified or explicit architecture of component species (Sinoquet and Caldwell, 1995, Louarn *et al.*, 2012). However, these studies focused on integrative parameters (height, LAI) which could not discriminate the effects of explicit architectural parameters defined at

the organ scale. As reported by several studies (Sinoquet and Caldwell, 1995, Barillot *et al.*, 2011, Barillot *et al.*, 2012, Louarn *et al.*, 2012), the present results further confirmed that light partitioning is strongly related to the ratio of the component species LAI and height. However, this relationship appeared to be dependent on the species considered and was not constant throughout the growing cycle. Light partitioning during the early stages of development was closely linked to the contribution of each component species to the LAI of the mixture. Species with high capacity for branching therefore displayed marked competitiveness for light capture. As the mixture grew, the interception of each plant started to be altered by its neighbours (*e.g.* foliage clumping, mutual shading) and inter-specific competition [for light] thus started to modify the relative importance of architectural parameters. When species started their vertical growth (internode elongation), the relationship between light partitioning and the ratio of the component species LAI was no longer linear. During later stages of the growing cycle, light partitioning tended to be related to height ratio. These results were consistent with a previous study carried out on virtual wheat–pea mixtures derived from the digitization of several pea cultivars grown under greenhouse conditions (Barillot *et al.*, 2012). The present work, based on dynamic models of both wheat and pea has therefore provided new information on the temporal variations of light partitioning throughout the growing cycle of the two species. Furthermore, the use of architectural models enabled us to assess the effects of specific parameters with respect to both wheat and pea architectures.

Leaf inclination also affected light partitioning but to a lesser extent than alterations to branching or internode length. This architectural trait does not appear to be a factor that should be targeted as a priority when manipulating the partitioning of light within mixtures. Nevertheless, Sarlikioti*et al.* (2011) reported that the leaf inclination of tomato impacted the distribution of light interception rather than total light interception. Further, the effect of leaf inclination should probably be related to plant height *i.e.* planophile leaves would

significantly improve the light interception of plants that are already the tallest in the mixture (see for example the alfalfa-tall fescue mixtures described by Barillot *et al.*, 2011). In our simulations based on wheat-pea mixtures, light partitioning was found to be highly sensitive to the number of tillers/branches and to internode length. Although they were significant, the effects of wheat internode length on light capture were less marked than in pea. Cici*et al.* (2008) also reported that in chickpea, changes to internode length did not lead to the strongest competition with sow thistle when compared to phyllochron variations, for example. By contrast, Lemerle*et al.* (2001) suggested that wheat plants with longer internodes had an enhanced competitive ability for light capture versus weeds. It therefore appears that an assessment of the effects of a given architectural parameter (*e.g.* branching, internode length or leaf inclination) on light partitioning should be carried out with respect to both: (i) the whole plant structure (*i.e.* other architectural parameters), and (ii) the morphogenesis of the neighbouring plant/species. Indeed, the determinant parameters that are known to affect light interception in pure stands (*e.g.* number of tillers or internode length) do not necessarily have the same quantitative effects in multi-specific stands, depending on the behaviour of the component species. Moreover, modifications made to branching and internode length triggered asymmetric variations in light partitioning, which means that: (i) other ranges of variation in architectural parameters should be tested in order to better explore the responses of light partitioning, and (ii) interactions with other parameters need to be taken into account *e.g.* leaf area distribution and clumping (Ross, 1981b, Lantinga *et al.*, 1999).

CONCLUSION

The questions addressed in this paper necessitated the development of a 3D and dynamic architectural model of pea (L-Pea) which, to our knowledge, is the first pea model to have become available in the literature. The L-Pea model is based on a deterministic approach that enabled the generation of simplified representations of pea architecture. Although they

may go beyond the scope of the present paper, further studies should be performed in order to obtain a more mechanistic approach to the modelling of pea morphogenesis. For instance, mechanistic rules could be implemented for branching, a process which is known to be closely dependent on genotype (Arumingtyas *et al.*, 1992, Barillot *et al.*, 2012) and environmental factors such as low temperatures (Jeudy and Munier-Jolain, 2005) and plant density (Spies *et al.*, 2010) and include the effects of light quality (Casal *et al.*, 1986, Ballaré and Casal, 2000). Integrating such responses in a model would nevertheless require the conduct of further studies in order to enhance our understanding of the regulation of branching and in particular how internal factors (*e.g.* hormone balance) respond to environmental signals (Evers *et al.*, 2011).

During the present study, the L-Pea model was used within a complex modelling framework that integrated an architectural model of wheat as well as a light model. Such virtual environments can facilitate approaches designed to define plant ideotypes adapted to intercropping by targeting morphological traits that need to be integrated in breeding programmes. Indeed, scaling the analysis at the organ level can facilitate links with geneticists and breeders. Taking the example of wheat–pea mixtures, several genes that govern pea architecture (branching, height, leaf-type) have already been identified (*e.g.* for pea, Arumingtyas *et al.*, 1992, Kusnadi *et al.*, 1992, Huyghe, 1998). For wheat (and other cereals), the studies performed during the green revolution also enabled the control of plant height (Evenson, 2003), notably by introducing dwarf genes (Hedden, 2003). Our study also highlighted the importance of considering plant architecture in the choice of the species/genotypes used for intercropping systems. Thus alongside standard criteria such as crop earliness, disease sensitivity and yield, attention should also be paid to the architectural traits involved in LAI and plant height. In particular, we showed that both branches and internode length are crucial architectural parameters that determine the ability of component

species to compete for light. Integration of these architectural traits should also take account of the fact that their impact on light partitioning will vary during the growing cycle, thus requiring greater better knowledge of the dynamic aspects of plant morphogenesis.

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FIGURES

Figure 1: Vertical profile of the final length of the wheat and pea internodes used in the reference simulation. The internode length of wheat is specified for the main stem (MS) and four tillers (T1 to T4).

Figure 2: Dynamics of LAI (A), plant height (B) and Light Interception Efficiency (LIE, C) in the reference simulation as a function of thermal time. These dynamics are shown for both the overall mixture and the component species (pea and wheat).

Figure 3: Relative variations in the LAI of pea (upper panel) and wheat (lower panel) estimated from the reference simulation. Variations were obtained by modifying the number of branches or tillers. The colour gradient indicates the amplitude of the modifications applied to the architectural parameters.

Figure 4: Relative variations in the height of pea (upper panel) and wheat (lower panel) estimated from the reference simulation. Variations were obtained by modifying the final length of internodes. The colour gradient indicates the amplitude of the modifications applied to the architectural parameters.

Figure 5: Dynamics (left) and relative variations (right, estimated from the reference simulation, in straight lines) of light partitioning (%PAR). %PAR is expressed as the fraction of light intercepted by a species (left and right axis for pea and wheat, respectively) over the total interception of the mixture. Therefore, %PAR values are complementary between pea and wheat and those of relative variations are the opposite. The number of branches, internode length and leaf inclination (for pea only) were altered for both pea (circles) and wheat (triangles) following the colour gradient.

Figure 6: Relationship between light partitioning (%PAR, ratio of light intercepted by one species to the overall interception of the mixture) and the species ratios of LAI (left) and height (right) at five particular stages of development. Variations in the ratios of LAI and height resulted from architectural alterations applied to pea (circles) and wheat (triangles) following the colour gradient.

TABLES

Table 1: Parameters of L-Pea model. Main stems are denoted as Axis-0 and branches are distinguished according to their nodal position on the main stem. Axis-1: branches developing at the first node; Axis-2: second node.

Module	Function	Parameters	Unit	Value	Source
Vegetative development	**Phytomer appearance rate**	R_L	phytomer°C° day^{-1}	**Axis-0**: 0.0165 **Axis-1**: 0.0183 **Axis-2**: 0.0171	Barillot *et al.*(2014)
		Phyto_final	phytomer	**Axis-0**: 11 **Axis-1**: 25 **Axis-2**: 20	Barillot *et al.*(2014)
	Branching	*nb_branch*	branch	**Axis-1**: 1.7 **Axis-2**: 1.6	Barillot *et al.*(2014)
		bud_break	C° day	**Axis-1**: 335 **Axis-2**: 289	Barillot *et al.*(2014)
Organ extension	**Organ length**	L_{final}	mm	-	Fitted to data [A]
		t_{base}	C day	**Internode:** 34.88 **Stipule:**0	Fitted to data [A]
		t_{max}	C day	**Internode:** 87.71 **Stipule:** 71.28	Fitted to data [A]
		t_{end}	C day	**Internode:** 171.51 **Stipule:** 197.66	Fitted to data [A]

Allometric coefficient	*k*	dimensionless	0.57	Fitted to data [A]
Senescence	*lifespan*	C day	480	Adapted from Lecoeur (2005)

[A] *See experiment described in Supplementary Information*

1

Table 2: Specific stages of the development of wheat and pea illustrated by side views of the virtual mixtures. The colour gradient is a function of the light intercepted by different organs (from blue to red).

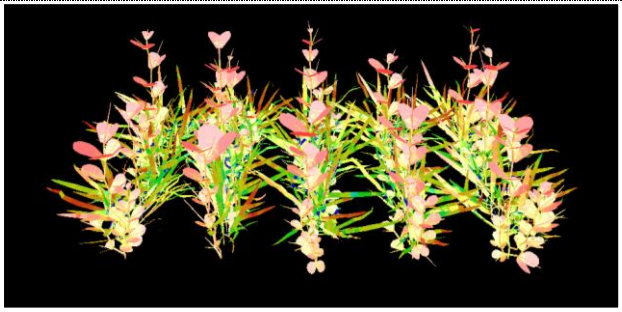
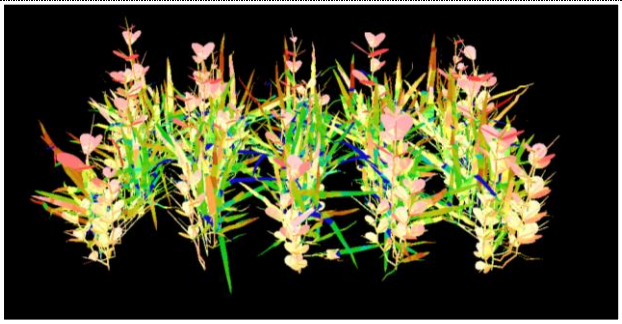
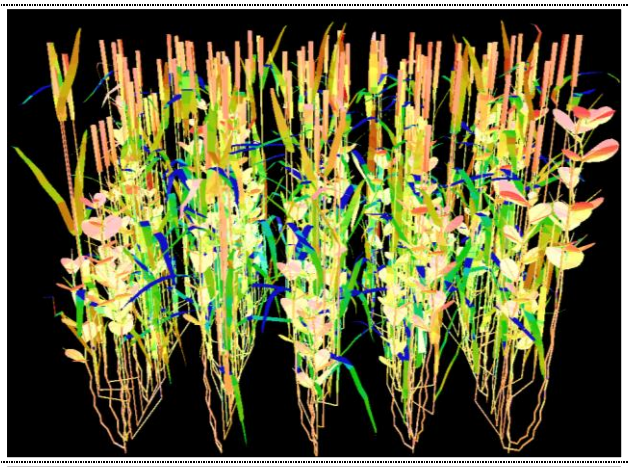
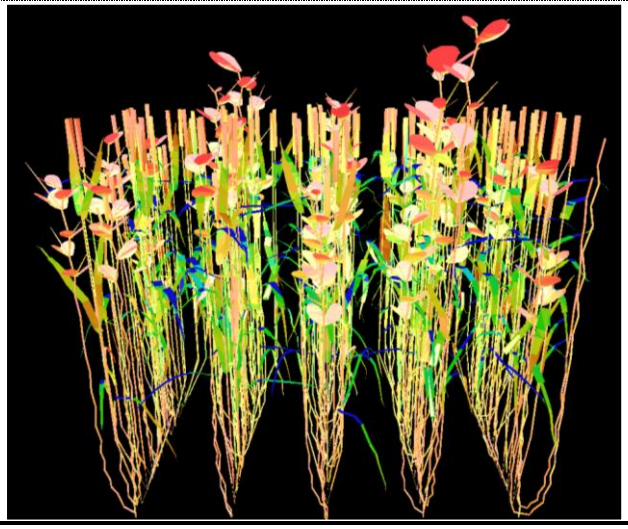
Snapshot	Thermal time (°C day)	Wheat	Pea
	500	4 unfolded leaves	4 unfolded leaves
	850	End of tillering	End of branching Branch elongation
	1000	Start of stem elongation	Branch elongation
	1500	Start of flowering	Flowering (not shown)
	2000	Grain filling Maturity	Maturity

Table 3: Input parameters of the ADEL-Wheat and L-Pea models as used for the reference simulation

Wheat		Pea		
Tillers	Internode length	Branches	Internode length	Leaf inclination (°)
4	See Figure 1	4	See Figure 1	45

1